Ecology Letters

WILEY

ECOLOGY LETTERS

LETTER

Migratory Strategy is a Key Factor Driving Interactions at Wind Energy Facilities in At-Risk North American Bats

Caitlin J. Campbell[1,2,3,4] | David M. Nelson[4] | Juliet Nagel[4,5] | Jeff Clerc[6] | Theodore J. Weller[7] | Jamin G. Wieringa[8] | Erin Fraser[9] | Fred J. Longstaffe[10] | Amanda M. Hale[5,11] | Meghan Lout[12] | Lori Pruitt[13] | Robert Guralnick[14] | Hannah B. Vander Zanden[2]

[1]Bat Conservation International, Austin, Texas, USA | [2]Department of Biology, University of Florida, Gainesville, Florida, USA | [3]Biodiversity Institute, University of Florida, Gainesville, Florida, USA | [4]Appalachian Laboratory, University of Maryland Center for Environmental Science, Frostburg, Maryland, USA | [5]Western Ecosystems Technology Inc., Cheyenne, Wyoming, USA | [6]National Renewable Energy Laboratory, Golden, Colorado, USA | [7]USDA Forest Service, Pacific Southwest Research Station, Arcata, California, USA | [8]U.S. Fish and Wildlife Service, Bloomington, Indiana, USA | [9]Memorial University of Newfoundland Grenfell Campus, Corner Brook, Newfoundland, Canada | [10]Department of Earth Sciences, The University of Western Ontario, London, Ontario, Canada | [11]Department of Biology, Texas Christian University, Fort Worth, Texas, USA | [12]VHB, South Burlington, Vermont, USA | [13]U.S. Fish and Wildlife Service (Retired), Bloomington, Indiana, USA | [14]Florida Museum of Natural History, Gainesville, Florida, USA

Correspondence: Caitlin J. Campbell (caitjcampbell@gmail.com)

Received: 2 September 2024 | **Revised:** 10 July 2025 | **Accepted:** 1 August 2025

Editor: Juan Manuel Morales

Funding: This work was supported by the Maryland Department of Natural Resources; the Ohio Division of Wildlife, Ohio Department of Natural Resources; and the U.S. Fish and Wildlife Service, F15AC00759.

Keywords: animal migration | green energy | hydrogen | movement ecology | stable isotopes | wind energy

ABSTRACT

Animal migration remains poorly understood for many organisms, impeding understanding of movement dynamics and limiting conservation actions. We develop a framework that scales from movements of individuals to the dynamics of continental migration using data synthesis of endogenous markers, which we apply to three North American bat species with unexplained high rates of fatalities at wind energy facilities. The two species experiencing the highest fatality rates exhibit a "pell-mell" migration strategy in which individuals move from summer habitats in multiple directions, both to higher and lower latitudes, during autumn. We link movements to higher latitudes to encounters with wind energy facilities and report that the timing of pell-mell migration strongly overlaps with that of fatalities at the continental level. These findings support the hypothesis that migration distance and strategy are drivers of increased interactions with wind energy facilities, highlighting the significance of understanding migratory strategy to achieve conservation goals.

1 | Introduction

Animal migration is a spectacular natural phenomenon responsible for the movements of trillions of organisms, thousands of species, and kilotons of nutrients across the Earth (Bauer and Hoye 2014). Yet, we know little about the migratory strategies of most organisms because many conventional techniques of studying migration are resource-intensive and limited to large and easily observed animals (Kays et al. 2015). Contrasting theories suggest that seasonal migration, here defined as a regular, repeated, and large-scale movement between different sites (Stern 2009), is motivated by individuals tracking consistent climatic niches or resources (Abrahms et al. 2021; Gómez et al. 2016; Jonzén et al. 2011). However, proximate drivers governed by social and behavioural factors, such as mating or ephemeral resource tracking, are not necessarily included in these general theories (Aikens et al. 2022; Burke et al. 2019). Moving beyond coarse-scale understanding of migratory dynamics for less well-studied taxa requires integrating complex individual-level behaviours to landscape-level shifts in the distributions of populations. New data types and analytical frameworks that scale from individuals to landscapes will both improve our understanding of animal migration and its drivers and likely uncover surprising and unique aspects of migration.

Migratory tree-roosting bats of North America (sensu Griffin 1970) are largely solitary, highly mobile, and notoriously difficult to study (Fleming and Eby 2003; Popa-Lisseanu and Voigt 2009). Their impressive capacity for long-distance movement is well known, but mostly anecdotal. For example, one species has colonised Hawaii, 3665 km from continental North America, and three are regular vagrants in Bermuda, 1064 km from mainland U.S. (Bonaccorso and McGuire 2013). Limited recapture data and location logging have shown long and often circuitous movements of a few individuals (> 1000 km; Morningstar and Sandilands 2019; Weller et al. 2016). Although migration theory predicts that niche or resource tracking would result in two discrete migratory periods between warm and cool seasons (Somveille et al. 2015), tree-roosting bats are most commonly observed migrating in the autumn and only infrequently in the springtime (Cryan 2003a; Findley and Jones 1964). Autumn flocks of eastern red bats were historically so expansive that they would reportedly remain visible overhead for days at a time (Howell 1908; Mearns 1898). Because tree-roosting species likely have sex-partitioned summer habitat (Findley and Jones 1964) and mate in the autumn, it has been suggested that mating behaviour could be a partial driver of autumn migratory patterns (Cryan et al. 2012; Cryan et al. 2006). However, the patterns and drivers of migratory strategy in tree-roosting bats have rarely been examined quantitatively nor across their entire geographic range and annual cycles, and thus remain largely unknown.

Better understanding of the migratory dynamics of these species is of pressing conservation importance because of unprecedented large-scale fatalities at wind energy facilities (Arnett et al. 2016). Collisions with the blades of wind turbines kill hundreds of thousands of bats in North America per year (Arnett and Baerwald 2013). A plurality of these fatalities (72%–79%) comprise just three migratory tree-roosting species, the hoary (*Lasiurus cinereus*; 32% of fatalities), eastern red (*Lasiurus borealis*; 24%), and silver-haired bats (*Lasionycteris noctivagans*; 16%; Allison and Butryn 2018; Thompson et al. 2017). Fatalities are concentrated in the late summer and early autumn suggesting a link to autumn migration (Arnett et al. 2008; Arnett and Baerwald 2013; Cryan and Brown 2007; Kunz et al. 2007). However, the link between turbine impacts and migration remains largely circumstantial, and much research focused on mitigating impacts to bat species focuses on proximal attractive factors (e.g., movement of nearby bats towards turbines; Cryan et al. 2022; Guest et al. 2022; though see Reusch et al. 2023). The rate of both existing and projected fatalities likely threatens the population viability of at least one species, the hoary bat (Frick et al. 2017; Friedenberg and Frick 2021). As wind energy development is increasing rapidly as a key part of the transition to renewable energy, the urgency to explain and mitigate these interactions is growing (Katzner et al. 2019).

Here we develop and apply a framework for understanding migration dynamics with a focus on North American tree-roosting bats, though our approach is applicable to other migratory animals (Figure 1). Our key methodological advance is integrating low-cost endogenous markers, in this case stable hydrogen isotope compositions of fur (Hobson et al. 2010), into a modelling framework that can reveal patterns of timing, distance, and direction of movement at a continental scale. The basis for this approach is that stable hydrogen isotope compositions of precipitation vary across geographic and climatic gradients in broadly latitudinal bands (Bowen et al. 2005). When the focal bats moult during early to mid-summer, their fur integrates isotopic compositions from the local environment where the fur is synthesised (Cryan et al. 2004; Fraser et al. 2017; Pylant et al. 2014). Thus, the stable hydrogen isotope compositions of the inert fur keratin reflect the summering location where fur was formed (Fraser et al. 2013). Isotope-based studies suggest that North American tree-roosting bats can be long-distance migrants, although with unclear overall patterns of migration (e.g., Cryan et al. 2014; Fraser et al. 2017). An advantage of our approach is the ability to synthesise large datasets comprising both new and published stable hydrogen isotope measurements transformed to a unified measurement scale. The increased sampling across broad spatial extents and across the annual cycle (Figure 2) provides a means to integrate spatial information across two scales: precise spatial and geographic information reflecting where and when tissue was sampled with more general estimates of the time and location of tissue formation. Our methodology accounts for variation inherent to sampling across multiple species, sampling locations and times, and analytical approaches. We applied our methodology, using measurements of endogenous markers from individuals, to infer population-level migratory behaviours for the three bat species most impacted by wind energy development in North America.

Our aims were to describe the migratory strategies of these species and explore whether they relate to ongoing interactions with wind energy facilities. First, we tested for patterns of sex-biased distributions of summering grounds, expecting to find females would select higher-latitude summer habitat than males and that this factor may inform overall migratory strategy. Second, we described the migratory patterns of each species, expecting to find patterns consistent with "to-and-fro migration" (Dingle and Drake 2007) between high-latitude summer habitats and lower-latitude winter habitats (Figure 3). Specifically, we expected to find that bats that spent the summer at higher latitudes would travel furthest and be more likely to move to lower latitudes to overwinter than counterparts that summered at lower latitudes. Because movement direction is inferred relative to the location where individuals grew their fur in the summer, we also expected to find strong evidence that when movement was detectable, isotopic evidence would show that most bats move to lower latitudes. Third, as a proxy for collision risk from turbines, we tested for differences in the movements of bats sampled at wind energy facilities versus by other methods (e.g., live captures; Figure 3). In each model, we account for key spatial, temporal, and geographic contexts, and thus unravel complex and counterintuitive signals of movement across the annual cycle

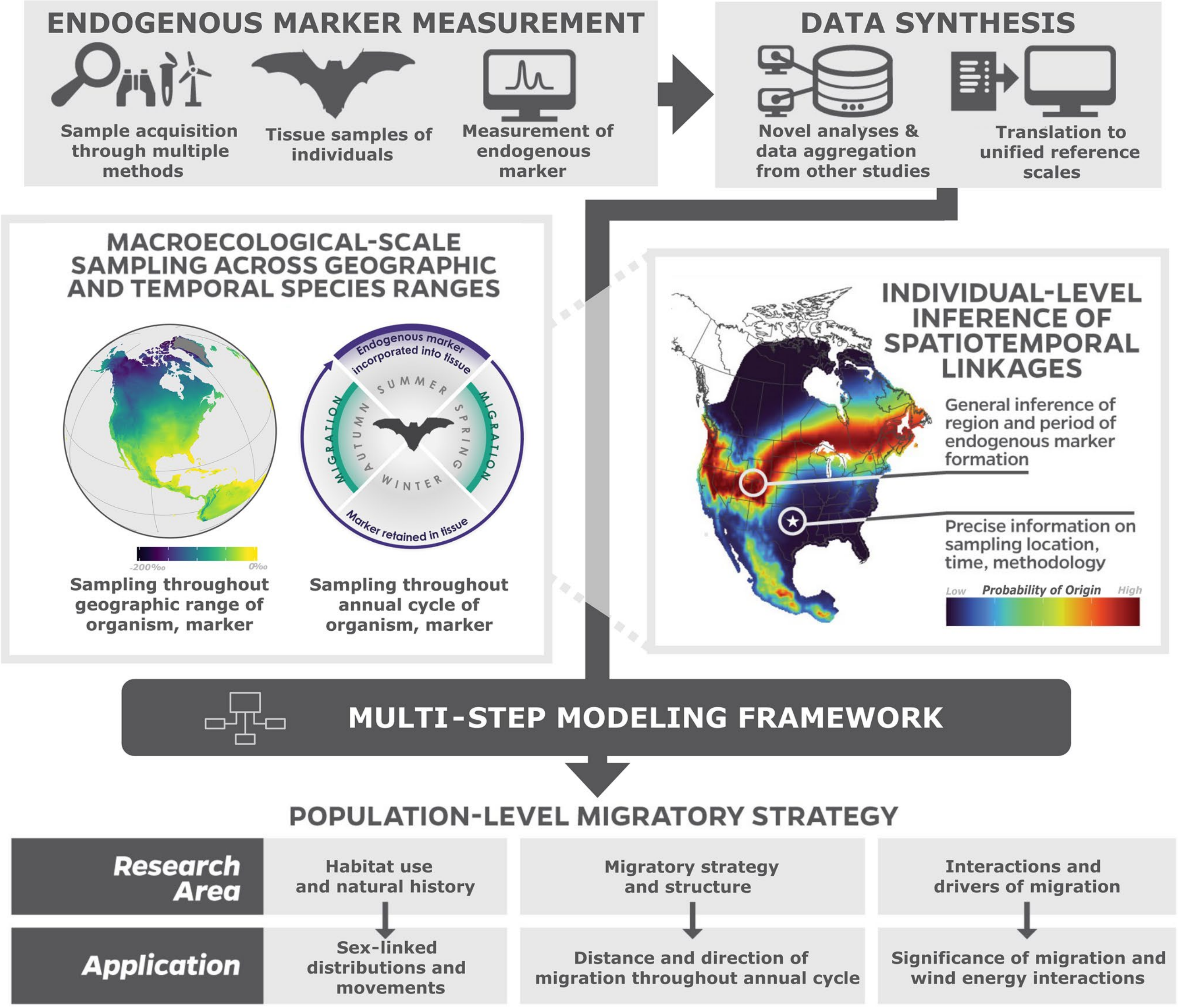

FIGURE 1 | A framework that scales from measurements of individual movements to the dynamics of continental migration. At top, individual organisms were sampled through multiple methods, including live capture as part of monitoring studies, museum specimens, and carcass searches at wind energy facilities. Samples were taken from individuals and analysed; in this study, bat fur samples were collected and analysed for stable hydrogen isotope compositions. Next, data synthesis was conducted to assimilate the endogenous marker data collected for this study with previously published data. Sampling was conducted broadly across the geographic ranges of the species and values of the marker (in this case, precipitation stable hydrogen isotope data); it was also conducted across the annual cycle of the organism. This widespread sampling enabled broad-scale individual-level inference of spatiotemporal linkages, by which precise information on sampling location, time, and methodology could be linked with general inferences about the region and period of tissue formation represented by the endogenous marker, in this case the location and timing of summer moult. Both sources of data were incorporated into a modelling framework through which research questions were explored. Here, we applied these research areas to answer specific questions on sex-linked distributions, distance and direction of movement, and significance of migration and its interactions with bat fatalities at wind energy facilities.

of seasonal migrants. This application of individual-level data synthesis to quantify migration at the macroecological scale provides insights into migratory strategies and potential risks to migratory organisms due to anthropogenic activities.

2 | Materials and Methods

This study comprised data collection, synthesis, and a multi-step modelling framework to test key research questions (Figure 1). First, we collected and analyzed fur samples for stable hydrogen isotope compositions (δ^2H) and synthesized these data with those of other studies. We then modeled the relationships between δ^2H values of fur and local precipitation to infer sample origins and created individual-level models of probable summer origin. Next, we extracted key summary statistics about individual movements from those models, relying primarily on the geographic and temporal relationships between the region and time of probable fur origin and the location and timing of sampling. We used those summary statistics as predictors in a modeling framework to identify drivers of sex-biased distributions, distance, and direction of travel. Finally, we tested whether bats

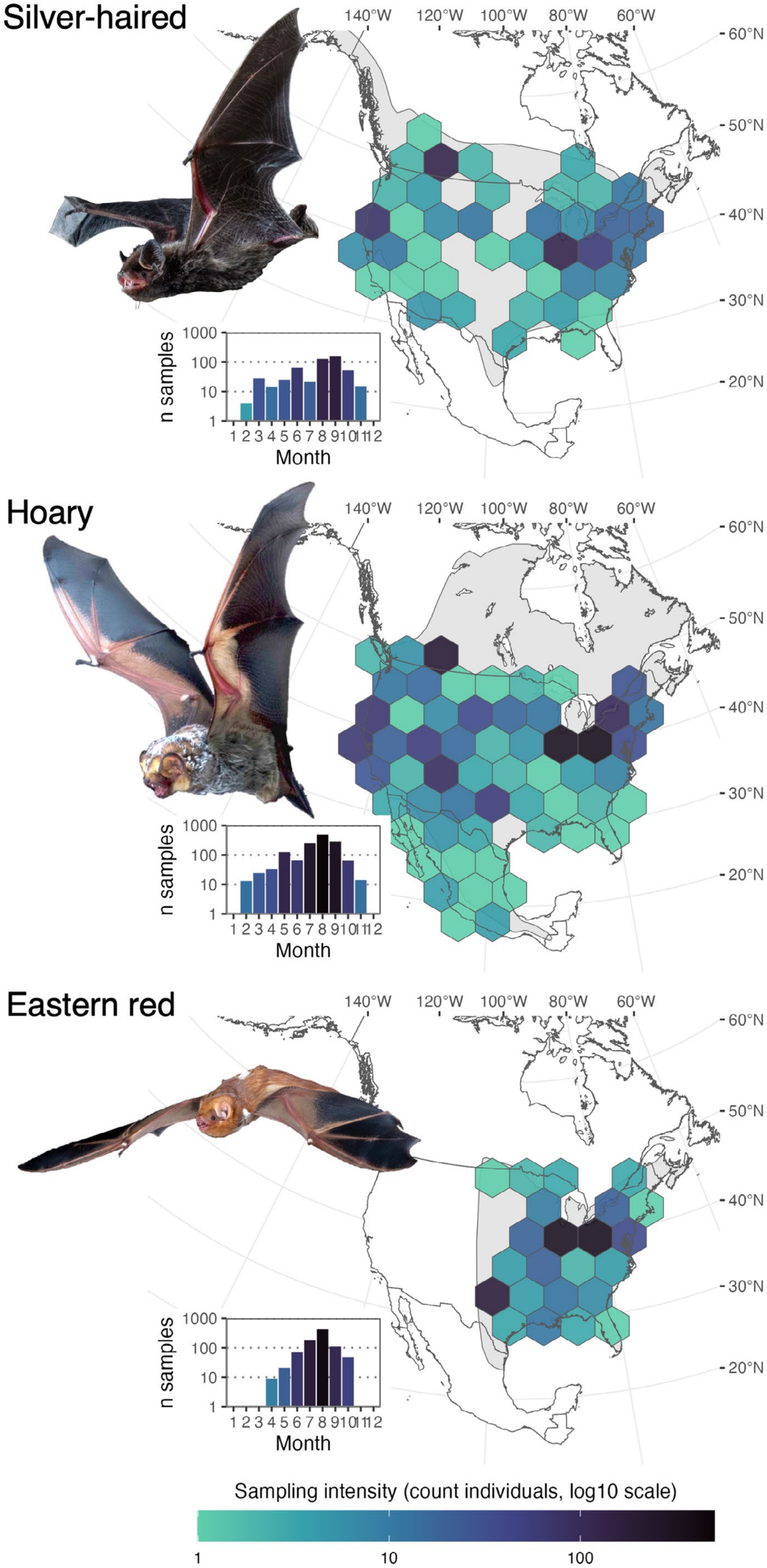

FIGURE 2 | Legend on next page.

FIGURE 2 | Samples were obtained from throughout the geographic ranges and across the annual cycle of each species. Panels highlight the sampling intensity for silver-haired, hoary, and eastern red bats, overlaid above species range maps (grey shading). Insets at bottom left of each panel show the number of fur samples obtained for each month of the calendar year (log10 scale). Photos by José G. Martínez-Fonseca and Sherri and Brock Fenton.

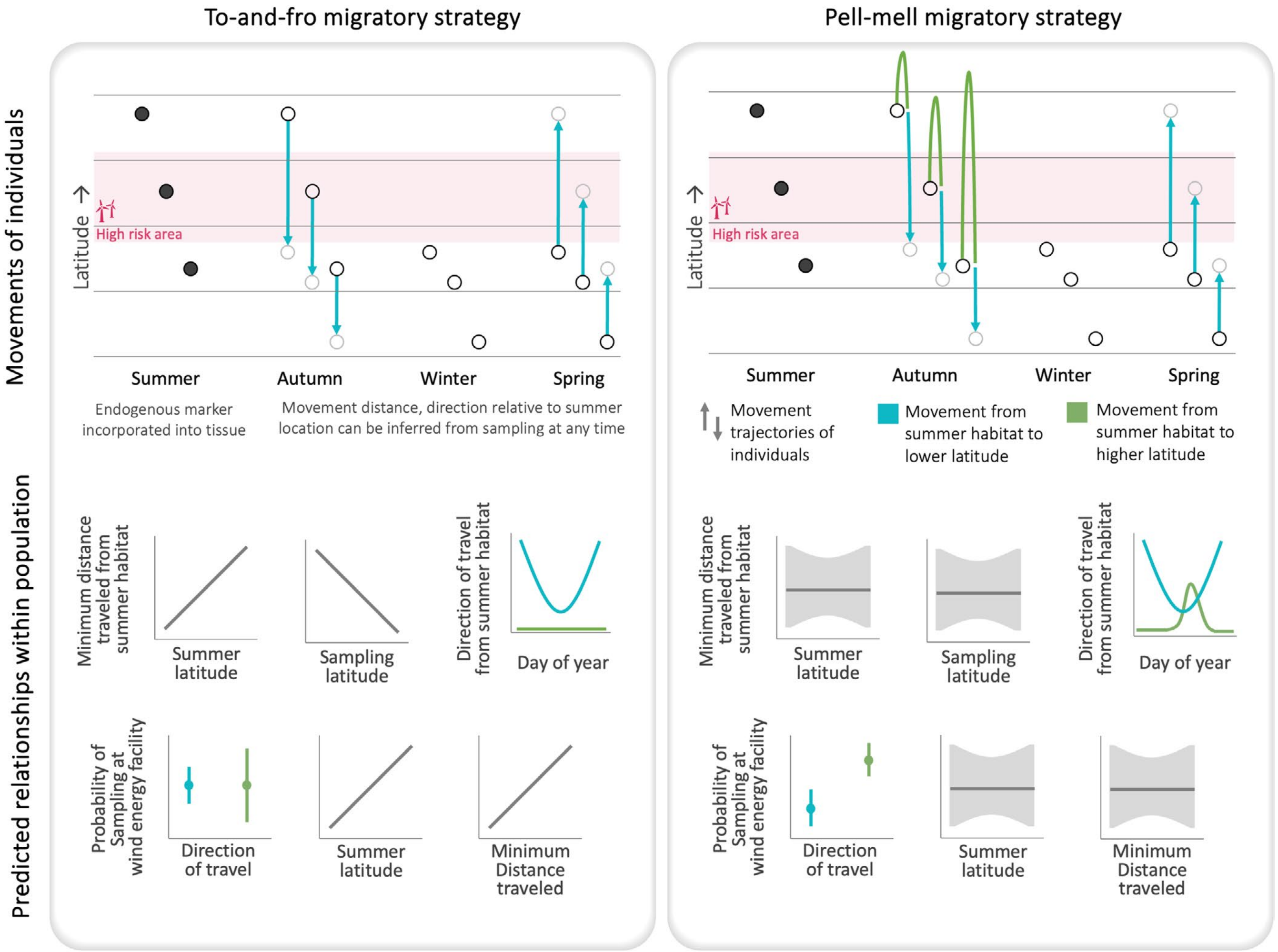

FIGURE 3 | A schematic of different migratory strategies over the annual cycle, highlighting the distance and direction of travel inferable from endogenous markers encoded in the summer as well as predicted relationships between key movement metrics and other factors. At top, a hypothetical population of three individuals begins at a summer habitat (closed circles), at which the endogenous marker was incorporated into tissue. Latitudinal movement from the start-of-season location (black open circles) to end-of-season location (grey open circles) is indicated by coloured lines (blue indicates movement that indicates, given sampling at a particular time, movement from summer habitat to lower latitude; green to higher). A hypothetical "high risk area" (pink shading) shows how pell-mell movements might increase the distance travelled by individuals within such a region, increasing risk exposure. The left column reflects a conventional to-and-fro migratory strategy; the right, an autumn pell-mell migratory strategy in which individuals move from summer habitat to both to higher and later lower latitudes in the autumn. The predicted relationships between individual-level movement characteristics and sampling metadata are highlighted in the lower panels. The expectation of no clear relationships is indicated by a horizontal line with a wide credible interval (grey shaded area).

sampled at wind energy facilities were associated with unique movement or distribution dynamics.

2.1 | Sample and Data Collection

We collected samples of fur from between the scapula of 1665 silver-haired ($n = 309$), hoary ($n = 719$), and eastern red bats ($n = 637$) for analysis of δ^2H values across North America. Most of these samples (84.7%) were obtained from carcasses salvaged at wind energy facilities, with the remainder coming from individuals that were captured alive. We integrated these new data with existing δ^2H values of fur for 1286 individuals sampled primarily from live capture and museum specimens (Baerwald et al. 2014; Cryan et al. 2004; Fraser et al. 2017; Pylant et al. 2014, 2016; Table S1). In total, the dataset used in our study comprises δ^2H values from 545 silver-haired, 1513 hoary, and 893 eastern red bats representing broad geographic and intra-annual temporal extents (Figure 2).

We compiled metadata associated with each individual, including species, morphology-based sex identification, geographic location of capture, and sampling method (e.g., carcass from wind energy monitoring, live-captured individual, or museum specimen). Geographic coordinates were compiled for each individual, either directly or through georeferencing locality descriptions.

2.2 | Assembly of New Hydrogen Stable Isotope Data

The 1665 fur samples for which stable hydrogen isotope analysis was performed in the present study were prepared as in Campbell et al. (2020). To account for exchange of keratin hydrogen with ambient vapour, we used comparative equilibration (Wassenaar and Hobson 2003) in which samples were analysed alongside matrix-matched international reference materials with known δ^2H values of non-exchangeable hydrogen and an internal standard. Fur samples were analysed for δ^2H values as described in detail in the Data S1.

2.3 | Assembly of Stable Hydrogen Isotope Data From Previous Studies

Isotopic compositions of samples from previous studies were generated using varying reference standards, many of which are laboratory-specific and, in some cases, not directly calibrated to the VSMOW-SLAP scale. To ensure data comparability, we used a previously described calibration chain transformation approach to assure comparable δ^2H_{fur} values across all previous studies and our newly generated dataset (Magozzi et al. 2021; Figure S1). This process is based on the measured relationships of δ^2H values among secondary standards, which are then used to calibrate different reference standard scales (Ma et al. 2020). At a later model step, we account for uncertainty introduced by this transformation (next section).

2.4 | Relating Fur and Precipitation δ^2H Values

The environmental drivers of spatial variation in δ^2H values of precipitation (δ^2H_{precip}) are well understood, but ecological and physiological factors cause δ^2H_{fur} values to shift as hydrogen is incorporated into animal tissues. To model the relationship between bat fur and local precipitation δ^2H values, we relied on the measured δ^2H_{fur} values of bats sampled during the period of fur growth for each species, as defined by prior studies (Cryan et al. 2014; Fraser et al. 2017; Pylant et al. 2016). We related each of these values to a modelled δ^2H value of precipitation at the sampling location, fitting a linear regression describing the predicted offset between δ^2H_{precip} and δ^2H_{fur} values for each species (Table S2). The use of this regression enables prediction of the geographic region of origin of a sample based on its measured δ^2H_{fur} value and the modelled distributions of δ^2H_{precip} values.

2.5 | Probability-of-Origin Map Creation and Interpretation

We used a multi-stage modelling framework to project the probability of origin for each sample of bat fur. These assignments were conducted using the isotopeAssignmentModel function in the R package isocat (Campbell 2020; Campbell et al. 2020). The output of this step is per-location probabilities of origin for each individual within each species' geographic range, stored as a raster.

We next applied a clustering framework to identify groups of individuals sharing similar summer geographic origins to others of the same species. The general approach, described in Campbell et al. (2020), is to compare each probability-of-origin surface within a species to each other, determine their relative similarity, and group individual origins based on that similarity. Groupings of individuals were partitioned using *k*-means (Figure S2). The clustered origins of each group were arranged in ascending mean aggregate latitude to ordinally represent the relative latitude of summer habitat compared to other origins from the same species.

Next, we calculated two key metrics to determine the characteristics of any detected movement by each individual: first, we measured the minimum distances travelled from summer origin to sampling location, and second, the latitudinal direction of movement between summer origin and sampling location (e.g., an individual might have moved from summer location to lower or to higher latitudes). Each summary metric was designed to account for the uncertainty within the geographic assignment of tissue origin, with distance travelled being calibrated by the performance of the metric for reference individuals and direction travelled using weighted subsampling to account for broad geographic areas of potential origins with similar likelihoods. Additional information on the calculation of these metrics is available in the Supplemental Methods.

2.6 | Statistical Analyses

We employed Bayesian generalised linear models to describe and investigate the migratory movements of the study species and potential relationships with geographic and demographic factors. We fit species-specific models with the following response variables: sex, distance of travel, latitudinal direction of travel, and whether the sample was obtained at a wind energy facility. All models were fit to predictors and interactions selected for likely biological relevance. For each response variable, we fit models to the same predictors across the three different species. All parameters were given weakly informative priors except for ordinal date in red bat models, which were informed from posterior distributions of the same parameters in the hoary bat. Models were fit in the probabilistic programming language STAN (Carpenter et al. 2017) using the R package brms (Bürkner 2017). We ran each model with 1000 iterations and a warmup of 500 iterations. We verified model convergence by confirming that no models had divergent transitions or r-hat statistics ≥ 1.05. We assessed model fit using posterior predictive checks to ensure models fit data assumptions.

We first fit a logit-link Bernoulli regression predicting identified sex on a dataset filtered to those with reliable sex identifications ($n = 220$, 426, and 214 for silver-haired, hoary, and eastern red bats respectively). Predictors were summer latitude, sampling latitude, second-order polynomial of ordinal date, and the interaction between sampling latitude and date.

We next fit models with minimum distance travelled as the response variable. Because this variable is zero-inflated and positive-skewed, we evaluated two families of hurdle model (log-linked gamma and log-normal). Predictor variables included summer latitude, sampling latitude, and second-order polynomial of ordinal date. We also evaluated competing models from both families with and without an interaction term between summer latitude and ordinal date. Model selection was performed using leave-one-out analysis, resulting in the selection of a top model with the lowest leave-one-out cross-validation score.

Our next model step estimated how the latitudinal direction of travel of individuals changed with respect to ordinal date. We summarised the direction of travel, which was categorised as whether individuals had moved from summer habitat to higher latitudes, to lower latitudes, or lacked evidence of movement. For each direction, we fitted a log-linked Bernoulli regression estimating the likelihood an individual had a detectable direction of movement as a function of a second-order polynomial of ordinal date.

Finally, we fit models estimating if sampling method, a binary parameter of whether samples were obtained at a wind energy facility or not, was affected by the movement of individual bats. Predictor variables for these models were direction of travel, minimum distance of travel, and summer latitude. We also fit additional comparative models using the probability of movement in a given direction, minimum distance of travel, and summer latitude as predictors. Finally, we examined the association between sampling method and the demographic parameters of age and sex, as well as whether age was related to movement to higher latitudes (Data S1).

3 | Results

3.1 | Evidence of Sex-Biased Latitudinal Distributions of Summer Habitat

We expected that females would be more likely to summer at higher latitudes than male bats, which we confirmed in silver-haired and hoary bats (silver-haired bat median posterior estimate 0.52, 95% credible interval [CI] 0.10–0.98; hoary bat 0.29, 95% CI 0.06–0.51). Female and male eastern red bats had no detected difference in summer distributions (−0.03, 95% CI −0.35 to 0.27; Table S3 and Figure S3).

3.2 | Unexpected Patterns of Distances Travelled for Hoary and Eastern Red Bats

We predicted that bats using a conventional migratory strategy that spent the summer at higher latitudes would have travelled further than those from low latitudes, and that bats sampled at low latitudes would have travelled less far than those from high latitudes (Figure 3). Silver-haired bats from higher summer latitudes had travelled further (median posterior estimate 0.50, 95% CI 0.38–0.62) and those sampled at low latitudes had travelled less far (−0.081, 95% CI −0.11 to −0.057; Figure 4a,b). Hoary bats that spent the summer at higher latitudes travelled further, though with a less strong relationship than silver-haired bats (0.19, 95% CI 0.13–0.25; Figure 4a). Hoary bats that spent the summer at lower latitudes travelled further than those from high latitudes (0.051, 95% CI 0.038–0.064; Figure 4b). Eastern red bats that spent the summer at high latitudes had travelled slightly further than those that had not (0.074, 95% CI 0.029–0.13). There was no relationship between sampling latitude and distances travelled for eastern red bats (−0.0020, 95% CI −0.017 to 0.014, Figure 4a,b and Table S4).

3.3 | Movements From Summer Locations to Both Higher and Lower Latitudes

We predicted that, in a conventional migratory strategy, the probability of movement from summer location to lower latitudes would be high, and at its maximum in the winter and minimum in the summer (i.e., form a U-shaped curve; Figure 3). Conversely, we expected that under a conventional migratory strategy, the probability of movement from summer habitat to higher latitudes would be very low and have no clear relationship with the day of the year. We found that the probability of movement to lower latitudes was common in all species, and that movement to higher latitudes was common in the late summer and early autumn in hoary and eastern red bats (Figure 4c–e). The probability of movement to lower latitudes peaked during the winter months with probabilities > 0.98 and 0.90 for the two species with samples representing most of the year, silver-haired and hoary bats respectively. Movement to higher latitudes was predicted with much higher probabilities for hoary and eastern red bats (peak probabilities of 0.32 and 0.30, respectively) than for silver-haired bats (peak predicted probability of 0.06). The probability of movement to higher latitudes for hoary bats was strongly unimodal, with the top 10% of predicted probabilities of movement in that direction occurring between days 206 and 239 (late July–late August). During this interval the probability of movement from summer habitat to higher latitudes was similar to that of lower latitudes, with movement to higher latitudes having a slightly higher predicted probability (Figure 4d). We found no evidence that the movement to higher or lower latitudes differed by sex (Table S6). The majority of bats moving from summer habitats to higher latitudes were adults, even when juvenile bats were common on the landscape (Figure S4; Supplemental Results).

3.4 | Associations With Sampling at Wind Energy Facilities

Silver-haired bats were similarly likely to have been sampled at wind energy facilities regardless of movements from summer habitat to higher or to lower latitudes (median estimate −0.15, 95% CI −1.58 to 1.11; Figure 5a). Hoary bats that moved from summer habitat to higher latitudes were more likely to be sampled at wind energy facilities than those that moved to lower latitudes (median estimate 1.67; 95% CI 1.21–2.11; Figure 5b). The median posterior estimate provided weak evidence that eastern red bats that moved from summer habitats to higher latitudes were more likely to have come from wind energy facilities than those that moved to lower latitudes (0.47), although the 95% credible interval of this estimate encompassed zero (CI −0.02 to 0.99; Figure 5c).

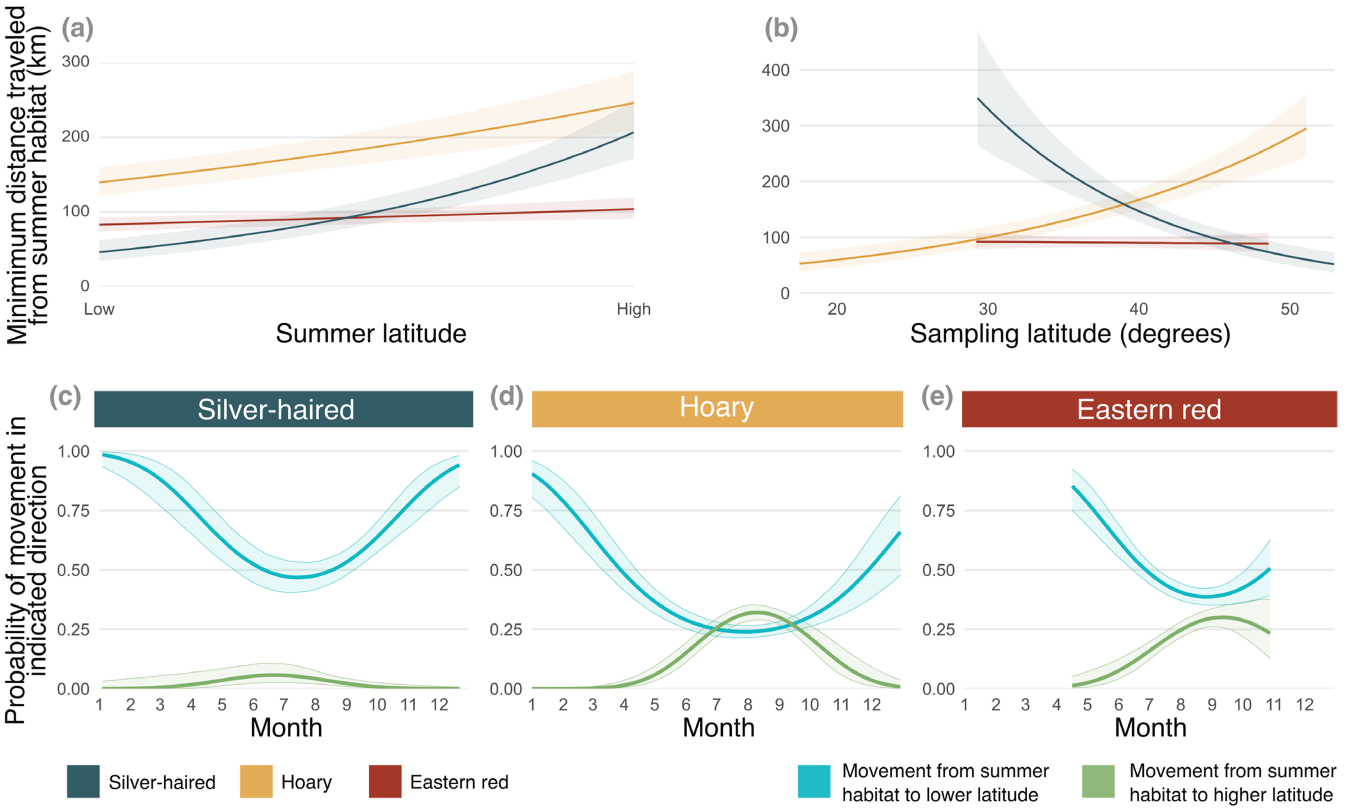

FIGURE 4 | The effect of summer latitude (a) and sampling latitude (b) on minimum distance travelled from summering grounds, and the effect of sampling month on probability of movement to higher and to lower latitudes (c–e). While silver-haired bats had movement distance and direction metrics consistent with a "to-and-fro" migratory strategy, hoary and eastern red bat movements were consistent with a "pell-mell" migratory strategy containing population-level movements to both higher and lower latitudes during the autumn. Model predictions reflect mean conditions for each species; lines indicate median estimate and shaded area 95% credible interval.

Silver-haired bats and eastern red bats that spent the summer at higher latitudes were more likely to have been sampled at a wind-energy facility than those that had not (silver-haired median estimate 0.54, 95% CI 0.37–0.73; eastern red 0.29, 95% CI 0.10–0.49). We observed no evidence of a relationship between summer latitude and sampling method observed for hoary bats (median estimate 0.10, 95% CI −0.06 to 0.25, Figure 5d and Table S7). Eastern red bats that travelled longer minimum distances were more likely to have been sampled at wind energy facilities than those that travelled shorter distances (median estimate 2.79e-3, 95% CI 1.04e-3–4.52e-3). Silver-haired and hoary bats had a positive relationship between minimum distance of travel and wind-related sampling, but these posterior estimates were imprecise and had large credible intervals (silver-haired median estimate 6.07e-4, 95% CI −2.20e-4 to 1.48e-3; hoary bat median estimate 3.55e-4, 95% CI −6.38e-5 to 7.99e-4; Figure 5e and Table S7).

4 | Discussion

4.1 | Discovery of a Pell-Mell Migratory Strategy

Our key finding is a migration pattern in which many hoary and eastern red bats move counter to the expected direction in the autumn, and travel from summer habitat to higher latitudes before ultimately reversing course to return to similar or lower latitudes to overwinter. Specifically, we identify three distinct range-wide migratory movements in hoary and eastern red bats: (1) migration from summer grounds to higher latitudes in late summer and early autumn; (2) a simultaneous or later migration to overwinter at generally lower latitudes, also in autumn; and (3) spring migration towards higher-latitude summering grounds. The co-occurrence of movement types 1 and 2, which results in widespread mixing of individuals on the landscape, results in a *pell-mell* migratory strategy in which individuals move widely and mix on the landscape in autumn. Two prior studies hinted at surprising "wandering" and circuitous autumn movements of four individual hoary bats (Morningstar and Sandilands 2019; Weller et al. 2016). Our dataset, comprising thousands of individuals, provides context for interpreting these tracking data as reflecting a broader migratory strategy. Our confidence in this characterisation is supported by contrasting results of silver-haired bat migration, which appear to follow a more conventional "to-and-fro" migratory strategy (patterns 2 and 3) consistent with climate- or resource-seeking movements. Although most long-distance animal migrations comprise individuals tracking seasonal shifts in temperature or general resource availability (Abrahms et al. 2021), movements to higher latitudes in autumn represent a migratory pattern likely motivated by other factors.

The autumn pell-mell strategy is more remarkable when considering that long-distance migration is both risky and

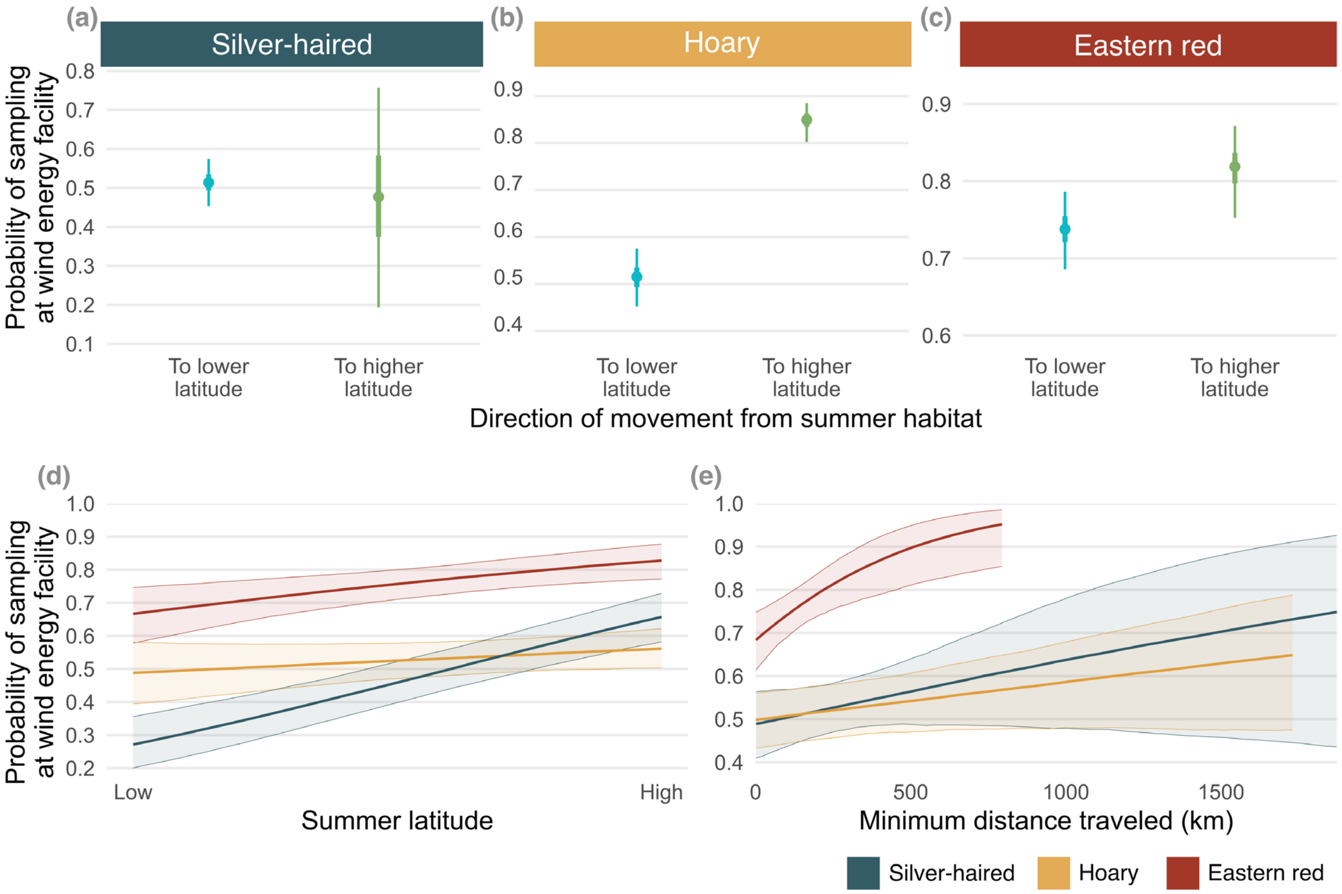

FIGURE 5 | Movement from summer habitat to higher latitudes is associated with increased probability of sampling at wind energy facilities for hoary and eastern red bats but not silver-haired bats (a–c). Probability of sampling at wind energy facilities also varied across species given differences in summer latitude and minimum distance travelled (d–e). In (a–c), the dot indicates median estimate, thicker line 50% credible interval (CI), and thin line 95% CI. Model predictions in (d, e) reflect mean conditions for each species; the line indicates median estimate and shaded area 95% CI.

energetically demanding, and most migrants pursue efficient routes to minimise energetic expenditure (Kranstauber et al. 2015). The strategy highlights the potential capacity of hoary and red bats to migrate many hundreds to thousands of kilometres, much farther than strictly necessary to seek favourable climatic conditions or food availability (Cryan 2003b; Weller et al. 2016). Adaptive strategies, including the use of torpor (Saugey et al. 1998; Weller et al. 2016) and feeding during migration (Krauel and McCracken 2013; Reimer et al. 2010; Valdez and Cryan 2009), may help them tolerate the energetic stresses of potentially travelling more than double the total distance between summer and winter habitats (Figure 3). We also note that because endogenous markers are only sensitive to movements that cross marker gradients, our approach is not sensitive to longitudinal movements and may be unreliable in signalling the presence of partial migration, both of which are expected in these species (Weller et al. 2016; Fleming 2019; Rogers et al. 2022). Our model results suggest that the vast majority of silver-haired and hoary bats likely overwinter at lower latitudes than where they spent the summer, although we were unable to infer this information clearly for eastern red bats due to limited winter sampling (Figure 2). Evaluating the interactions of bioclimatic, social and behavioural, and physiological factors governing the capacities and decisions of individuals to migrate remains a promising future area of research (Alerstam et al. 2003; Auteri 2022).

We found strong evidence of sex-differentiated summer distributions in all three species, a factor that might drive the multi-directional pell-mell autumn migration in hoary and red bats. Our results show that female bats were more likely than males to summer in high-latitude areas (Figure S3), supporting evidence of sex-biased migration that was previously inferred from occurrence records (Cryan 2003a; Findley and Jones 1964) and habitat suitability models (Hayes et al. 2015). All three species mate in the autumn, prior to or during autumn migration (Cryan et al. 2012). Although we found that summer distributions are generally biased by sex, autumn pell-mell movements appear to be undertaken by both sexes (Table S6). We expect that male bats may be incentivised to search for mating opportunities at higher latitudes than their summering grounds, either by seeking mates directly or travelling to hypothesised lekking or swarming locations (Cryan et al. 2012, 2006; Fraser and McGuire 2023). Female bats must also be incentivised to move in late summer, potentially to either seek out or avoid mating events, or possibly to pursue favourable prey availability after an interval of low mobility while raising young. An alternate potential driver of movements may be the mass emergences of migratory insect prey (Kotila et al. 2023; Rydell et al. 2010). Although such migratory events have been poorly characterised in North America, they could represent a spike in food availability in terms of thousands of tons of biomass (Hu et al. 2016). Prey seeking and weather conditions have been proposed as a driver of autumn movements towards higher latitudes by bats in Europe (Voigt et al. 2023), which may also represent a pell-mell migratory behaviour in a different species of migratory bat.

4.2 | Migratory Behaviour as a Driver of Anthropogenic Interactions

Our results provide the first direct support for the hypothesis that migration is a key driver of bat fatalities at wind energy facilities, and suggest that the length of migratory routes is a key risk factor governing encounter rates with wind energy facilities. To date, links of migratory behaviour to wind energy impacts have been made circumstantially through the phenological overlap of autumn migration and peaks in bat fatalities at wind energy facilities (Allison and Butryn 2018; Cryan and Barclay 2009; Cryan and Brown 2007). As migratory species may be more inclined to encounter or forage at the heights of wind turbines generally (Roeleke et al. 2016; Roemer et al. 2017), it has remained challenging to disentangle processes driving fatalities from correlated factors. Here, we demonstrate that the timing of the interval in which hoary and eastern red bats are regularly found to have moved summer locations to both higher and lower latitudes—likely representing an interval of widespread multi-directional movements by these species—coincides with the timing of fatalities. Further, we found that movements to higher latitudes and longer minimum travel distances are both associated with samples obtained at wind energy facilities (Figure 5). This further supports our conclusion that migration distance and pell-mell migration strategy are both key drivers of bat fatalities at wind energy facilities, as increased migration distance presumably increases general likelihoods of individuals encountering turbines.

Although substantial research has focused on bat attraction to nearby wind turbines (Cryan et al. 2022; Cryan and Barclay 2009; Foo et al. 2017; Guest et al. 2022; Kunz et al. 2007; Reimer et al. 2018), our findings indicate that pell-mell migration may increase the number of turbines a bat is likely to encounter. As many hoary and eastern red bats move from summer habitat to higher latitudes and eventually move to lower latitudes to overwinter, the routes travelled by those migrants would be significantly greater than that of bats migrating in one direction to overwinter (to-and-fro migration; Figure 3). Thus, hoary and eastern red bats appear much more likely to encounter more obstacles during their seasonal movements. Simply put, their migratory behaviour results in many more opportunities to encounter wind turbines than do species that do not engage in a long, likely circuitous migration (Weller et al. 2016). This factor may help to explain why bat fatalities at U.S. and Canada wind energy facilities comprise predominantly hoary (32%) and eastern red bats (24%), while other migratory species are less impacted (e.g., the silver-haired [16%] and tricolored bats [*Perimyotis subflavus*, 2%]; Allison and Butryn 2018). Further, if individuals migrating during autumn are at greatest risk of encountering wind turbines, that provides an explanation for why monitoring warm-season bat activity and modelling habitat suitability are not necessarily strong predictors of bat fatality rates (Bennett and Hale 2018; Solick et al. 2020).

4.3 | A Generalizable Framework

Migration drives broad changes to biodiversity and shifts in ecosystem dynamics worldwide, but our knowledge of migration patterns and strategy for most taxa is limited. Here, we implemented a framework for unravelling migratory strategy and its interactions from the sampling of endogenous markers of individual organisms. Such approaches are growing in popularity and include applications with stable isotopes, trace elements, genetics, and trait-based markers (Brewer et al. 2021; Rushing et al. 2014; Vander Zanden et al. 2018; Wieringa et al. 2020). By sampling with the greatest possible breadth with respect to the geographic range of the species, geographic variance of the marker, and annual cycle of both the species and the endogenous marker, we built a model using data from thousands of individuals to represent migratory strategy over the entire population and annual cycle of the species. We performed data synthesis which translated data collected at multiple laboratories to a unified reference scale. We also accounted for model error iteratively throughout the modelling process, both within the origin mapping steps and at multiple stages when collecting summary statistics. This framework was then leveraged to provide insight into natural history, migratory strategy, and interactions and drivers of migration. We anticipate that this approach will be applicable to a diversity of taxa across the Tree of Life.

Author Contributions

C.J.C., D.M.N., and H.B.V.Z. conceptualised and designed the study; C.J.C., D.M.N., J.N., J.C., T.J.W., E.F., F.J.L., A.H., M.L., and L.P. collected data; C.J.C., D.M.N., and H.B.V.Z. analysed data; C.J.C., D.M.N., R.G., and H.B.V.Z. wrote the paper; all authors revised the paper and approved its submission.

Acknowledgements

We would like to thank those involved in obtaining, sharing, and analysing the samples used in this study; particular thanks to Robin Paulman, Regina Trott, Carlyle Meekins, Scott Osborn, Elizabeth Stevenson, J. Edward Gates, Cortney Pylant, Becky Johnson, Carl Herzog, Jason Williams, Anna Weaver, Greg Aldrich, J. Paul White, Dave S. Johnston, Charles Brown, Carly RW Kalina, Lisle Gibbs, and Bryan Carstens. We thank Michael Belitz, Ana Longo, Robert Fletcher, Todd Katzner, and three anonymous reviewers for their valuable feedback on the methodology and manuscript. This work was funded by the Maryland Department of Natural Resources and the U.S. Fish and Wildlife Service, as well as by a grant from the Competitive State Wildlife Grants Program to Ohio State University and the University of Maryland Center for Environmental Science as jointly administered by the U.S. Fish and Wildlife Service, the Ohio Division of Wildlife and the Maryland Department of Natural Resources. C.J.C. was supported by a University of Florida Graduate School Funding Award, a University of Florida Biodiversity Institute Fellowship, and a Threadgill Dissertation Fellowship. This work was authored in part by the National Renewable Energy Laboratory, operated by Alliance for Sustainable Energy LLC, for the U.S. Department of Energy Wind Energy Technologies Office. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service, the

Departments of Agriculture or Energy, or the U.S. Government. The U.S. Government retains—and the publisher, by accepting the article for publication, acknowledges—that the U.S. Government retains a nonexclusive, paid-up, irrevocable, worldwide licence to publish or reproduce the published form of this work, or allow others to do so, for U.S. Government purposes.

Data Availability Statement

The data and code that support the findings of this study are openly available on Zenodo at https://doi.org/10.5281/zenodo.10578031.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70202.

References

Abrahms, B., E. O. Aikens, J. B. Armstrong, W. W. Deacy, M. J. Kauffman, and J. A. Merkle. 2021. "Emerging Perspectives on Resource Tracking and Animal Movement Ecology." *Trends in Ecology & Evolution* 36: 308–320.

Aikens, E. O., I. D. Bontekoe, L. Blumenstiel, A. Schlicksupp, and A. Flack. 2022. "Viewing Animal Migration Through a Social Lens." *Trends in Ecology & Evolution* 37: 985–996.

Alerstam, T., A. Hedenstrom, S. Akesson, A. Hedenström, and S. Åkesson. 2003. "Long-Distance Migration: Evolution and Determinants." *Oikos* 103: 247–260.

Allison, T., and R. Butryn. 2018. *A Summary of Bat Fatality Data in a Nationwide Database*. American Wind Wildlife Institute.

Arnett, E. B., and E. F. Baerwald. 2013. "Impacts of Wind Energy Development on Bats: Implications for Conservation." In *Bat Evolution, Ecology, and Conservation*, edited by R. A. Adams and S. C. Pedersen, 435–456. Springer.

Arnett, E. B., E. F. Baerwald, F. Mathews, et al. 2016. "Impacts of Wind Energy Development on Bats: A Global Perspective." In *Bats in the Anthropocene: Conservation of Bats in a Changing World*, edited by C. C. Voigt, and T. Kingston, 295–323. Springer.

Arnett, E. B., W. K. Brown, W. P. Erickson, et al. 2008. "Patterns of Bat Fatalities at Wind Energy Facilities in North America." *Journal of Wildlife Management* 72: 61–78.

Auteri, G. G. 2022. "A Conceptual Framework to Integrate Cold-Survival Strategies: Torpor, Resistance and Seasonal Migration." *Biology Letters* 18: 20220050.

Baerwald, E. F. F., W. P. P. Patterson, and R. M. R. Barclay. 2014. "Origins and Migratory Patterns of Bats Killed by Wind Turbines in Southern Alberta: Evidence From Stable Isotopes." *Ecosphere* 5: 1–17.

Bauer, S., and B. J. Hoye. 2014. "Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide." *Science* 344: 1242552.

Bennett, V. J., and A. M. Hale. 2018. "Resource Availability May Not Be a Useful Predictor of Migratory Bat Fatalities or Activity at Wind Turbines." *Diversity* 10: 44.

Bonaccorso, F. J., and L. P. McGuire. 2013. "Modeling the Colonization of Hawai by Hoary Bats (*Lasiurus cinereus*)." In *Bat Evolution, Ecology, and Conservation*, edited by R. A. Adams and S. C. Pedersen, 187–205. Springer.

Bowen, G. J., L. I. Wassenaar, and K. a. Hobson. 2005. "Global Application of Stable Hydrogen and Oxygen Isotopes to Wildlife Forensics." *Oecologia* 143: 337–348.

Brewer, C. T., W. A. Rauch-Davis, and E. E. Fraser. 2021. "The Use of Intrinsic Markers for Studying the Migratory Movements of Bats." *Animals* 11: 3477.

Burke, R. A., J. K. Frey, A. Ganguli, and K. E. Stoner. 2019. "Species Distribution Modelling Supports "Nectar Corridor" Hypothesis for Migratory Nectarivorous Bats and Conservation of Tropical Dry Forest." *Diversity and Distributions* 25: 1399–1415.

Bürkner, P. C. 2017. "brms: An R Package for Bayesian Multilevel Models Using STAN." *Journal of Statistical Software* 80: 1–28.

Campbell, C. 2020. Isocat: Isotope Origin Clustering and Assignment Tools.

Campbell, C. J., M. C. Fitzpatrick, H. B. Vander Zanden, and D. M. Nelson. 2020. "Advancing Interpretation of Stable Isotope Assignment Maps: Comparing and Summarizing Origins of Known-Provenance Migratory Bats." *Animal Migration* 7: 27–41.

Carpenter, B., A. Gelman, M. D. Hoffman, et al. 2017. "Stan: A Probabilistic Programming Language." *Journal of Statistical Software* 76: 1–32.

Cryan, P., J. Jameson, E. Baerwald, et al. 2012. "Evidence of Late-Summer Mating Readiness and Early Sexual Maturation in Migratory Tree-Roosting Bats Found Dead at Wind Turbines." *PLoS One* 7: e47586.

Cryan, P. M. 2003a. "Seasonal Distribution of Migratory Tree Bats (Lasiurus and Lasionycteris) in North America." *Journal of Mammalogy* 84: 579–593.

Cryan, P. M. 2003b. "Sex Differences in the Thermoregulation and Evaporative Water Loss of a Heterothermic Bat, *Lasiurus cinereus*, During Its Spring Migration." *Journal of Experimental Biology* 206: 3381–3390.

Cryan, P. M., and R. M. R. Barclay. 2009. "Causes of Bat Fatalities at Wind Turbines: Hypotheses and Predictions." *Journal of Mammalogy* 90: 1330–1340.

Cryan, P. M., R. M. R. Barclay, E. B. Arnett, et al. 2006. "Mating Behavior as a Possible Cause of Bat Fatalities at Wind Turbines. An Annual Report Prepared for the Bats and Wind Energy Cooperative." *Journal of Wildlife Management* 14: 1330–1340.

Cryan, P. M., M. A. Bogan, R. O. Rye, G. G. P. Landis, and C. L. Kester. 2004. "Stable Hydrogen Isotope Analysis of Bat Hair as Evidence for Seasonal Molt and Long-Distance Migration." *Journal of Mammalogy* 85: 995–1001.

Cryan, P. M., and A. C. Brown. 2007. "Migration of Bats Past a Remote Island Offers Clues Toward the Problem of Bat Fatalities at Wind Turbines." *Biological Conservation* 139: 1–11.

Cryan, P. M., P. M. Gorresen, B. R. Straw, S. S. Thao, and E. DeGeorge. 2022. "Influencing Activity of Bats by Dimly Lighting Wind Turbine Surfaces With Ultraviolet Light." *Animals* 12: 9.

Cryan, P. M., C. A. Stricker, and M. B. Wunder. 2014. "Continental-Scale, Seasonal Movements of a Heterothermic Migratory Tree Bat." *Ecological Applications* 24: 602–616.

Dingle, H., and V. A. Drake. 2007. "What Is Migration?" *Bioscience* 57, no. 2: 113–121.

Findley, J. S., and C. Jones. 1964. "Seasonal Distribution of the Hoary Bat." *Journal of Mammalogy* 45: 461–470.

Fleming, T. H. 2019. "Bat Migration." *Encyclopedia of Animal Behavior* Volume 3: 605–610.

Fleming, T. H., and P. Eby. 2003. "Ecology of Bat Migration." In *Bat Ecology*, 156–208. Springer Science & Business Media.

Foo, C. F., V. J. Bennett, A. M. Hale, J. M. Korstian, A. J. Schildt, and D. A. Williams. 2017. "Increasing Evidence That Bats Actively Forage at Wind Turbines." *PeerJ* 5: e3985.

Fraser, E. E., D. Brooks, and F. J. Longstaffe. 2017. "Stable Isotope Investigation of the Migratory Behavior of Silver-Haired Bats (*Lasionycteris noctivagans*) in Eastern North America." *Journal of Mammalogy* 38: 2067–2069.

Fraser, E. E., F. J. Longstaffe, and M. B. Fenton. 2013. "Moulting Matters: The Importance of Understanding Moulting Cycles in Bats When Using Fur for Endogenous Marker Analysis." *Canadian Journal of Zoology* 91: 533–544.

Fraser, E. E., and L. P. McGuire. 2023. "Prehibernation Swarming in Temperate Bats: A Critical Transition Between Summer Activity and Hibernation." *Canadian Journal of Zoology* 101: 408–422.

Frick, W. F., E. F. Baerwald, J. F. Pollock, et al. 2017. "Fatalities at Wind Turbines May Threaten Population Viability of a Migratory Bat." *Biological Conservation* 209: 172–177.

Friedenberg, N. A., and W. F. Frick. 2021. "Assessing Fatality Minimization for Hoary Bats Amid Continued Wind Energy Development." *Biological Conservation* 262: 109309.

Gómez, C., E. A. Tenorio, P. Montoya, and C. D. Cadena. 2016. "Niche-Tracking Migrants and Niche-Switching Residents: Evolution of Climatic Niches in New World Warblers (Parulidae)." *Proceedings of the Royal Society B: Biological Sciences* 283: 20152458.

Griffin, D. R. 1970. "Migration and Homing of Bats." In *Biology of Bats*, 233–264. Elsevier.

Guest, E. E., B. F. Stamps, N. D. Durish, et al. 2022. "An Updated Review of Hypotheses Regarding Bat Attraction to Wind Turbines." *Animals* 12: 343.

Hayes, M. A., P. M. Cryan, and M. B. Wunder. 2015. "Seasonally-Dynamic Presence-Only Species Distribution Models for a Cryptic Migratory Bat Impacted by Wind Energy Development." *PLoS One* 10: e0132599.

Hobson, K. A., R. Barnett-Johnson, and T. Cerling. 2010. "Using Isoscapes to Track Animal Migration." In *Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping*, 273–298. Springer.

Howell, A. H. 1908. "Notes on the Diurnal Migrations of Bats." *Proceedings of the Biological Society of Washington* 21: 35–38.

Hu, G., K. S. Lim, N. Horvitz, et al. 2016. "Mass Seasonal Bioflows of High-Flying Insect Migrants." *Science* 354: 1584–1587.

Jonzén, N., E. Knudsen, R. D. Holt, and B.-E. Sæther. 2011. "Uncertainty and Predictability: The Niches of Migrants and Nomads." In *Animal Migration: A Synthesis*, edited by E. J. Milner-Gulland, J. M. Fryxell, and A. R. Sinclair. OUP Oxford.

Katzner, T. E., D. M. Nelson, J. E. Diffendorfer, et al. 2019. "Wind Energy: An Ecological Challenge." *Science* 366: 1206–1207.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski. 2015. "Terrestrial Animal Tracking as an Eye on Life and Planet." *Science* 348: aaa2478.

Kotila, M., K. M. Suominen, V. V. Vasko, et al. 2023. "Large-Scale Long-Term Passive-Acoustic Monitoring Reveals Spatio-Temporal Activity Patterns of Boreal Bats." *Ecography* 2023: e06617.

Kranstauber, B., R. Weinzierl, M. Wikelski, and K. Safi. 2015. "Global Aerial Flyways Allow Efficient Travelling." *Ecology Letters* 18: 1338–1345.

Krauel, J. J., and G. F. McCracken. 2013. "Recent Advances in Bat Migration Research." In *Bat Evolution, Ecology, and Conservation*, edited by R. A. Adams and S. C. Pedersen, 293–313. Springer.

Kunz, T. H., E. B. Arnett, W. P. Erickson, et al. 2007. "Ecological Impacts of Wind Energy Development on Bats: Questions, Research Needs, and Hypotheses." *Frontiers in Ecology and the Environment* 5: 315–324.

Ma, C., H. B. V. Zanden, M. B. Wunder, and G. J. Bowen. 2020. "assignR: An R Package for Isotope-Based Geographic Assignment." *Methods in Ecology and Evolution* 11: 996–1001.

Magozzi, S., C. P. Bataille, K. A. Hobson, et al. 2021. "Calibration Chain Transformation Improves the Comparability of Organic Hydrogen and Oxygen Stable Isotope Data." *Methods in Ecology and Evolution* 12: 732–747.

Mearns, E. A. 1898. *A Study of the Vertebrate Fauna of the Hudson Highlands: With Observations on the Mollusca, Crustacea, Lepidoptera, and the Flora of the Region*. American Museum of Natural History.

Morningstar, D., and A. Sandilands. 2019. "Summer Movements of a Radio-Tagged Hoary Bat (*Lasiurus Cinereus*) Captured in Southwestern Ontario." *Canadian Field-Naturalist* 133: 125–129.

Popa-Lisseanu, A. G., and C. C. Voigt. 2009. "Bats on the Move." *Journal of Mammalogy* 90: 1283–1289.

Pylant, C. L., D. M. Nelson, M. C. Fitzpatrick, J. E. Gates, and S. R. Keller. 2016. "Geographic Origins and Population Genetics of Bats Killed at Wind-Energy Facilities." *Ecological Applications* 26: 1381–1395.

Pylant, C. L., D. M. Nelson, S. R. Keller, and P. Gandini. 2014. "Stable Hydrogen Isotopes Record the Summering Grounds of Eastern Red Bats (*Lasiurus borealis*)." *PeerJ* 2: e629.

Reimer, J. P., E. F. Baerwald, and R. M. R. Barclay. 2010. "Diet of Hoary (*Lasiurus cinereus*) and Silver-Haired (*Lasionycteris noctivagans*) Bats While Migrating Through Southwestern Alberta in Late Summer and Autumn." *American Midland Naturalist* 164: 230–237.

Reimer, J. P., E. F. Baerwald, and R. M. R. Barclay. 2018. "Echolocation Activity of Migratory Bats at a Wind Energy Facility: Testing the Feeding-Attraction Hypothesis to Explain Fatalities." *Journal of Mammalogy* 99: 1472–1477.

Reusch, C., A. A. Paul, M. Fritze, S. Kramer-Schadt, and C. C. Voigt. 2023. "Wind Energy Production in Forests Conflicts With Tree-Roosting Bats." *Current Biology* 33: 737–743.e3.

Roeleke, M., T. Blohm, S. Kramer-Schadt, Y. Yovel, and C. C. Voigt. 2016. "Habitat Use of Bats in Relation to Wind Turbines Revealed by GPS Tracking." *Scientific Reports* 6, no. 1: 28961.

Roemer, C., T. Disca, A. Coulon, and Y. Bas. 2017. "Bat Flight Height Monitored From Wind Masts Predicts Mortality Risk at Wind Farms." *Biological Conservation* 215: 116–122.

Rogers, E. J., L. McGuire, F. J. Longstaffe, J. Clerc, E. Kunkel, and E. Fraser. 2022. "Relating Wing Morphology and Immune Function to Patterns of Partial and Differential Bat Migration Using Stable Isotopes." *Journal of Animal Ecology* 91, no. 4: 858–869.

Rushing, C. S., T. B. Ryder, J. F. Saracco, and P. P. Marra. 2014. "Assessing Migratory Connectivity for a Long-Distance Migratory Bird Using Multiple Intrinsic Markers." *Ecological Applications* 24: 445–456.

Rydell, J., L. Bach, M. J. Dubourg-Savage, M. Green, L. Rodrigues, and A. Hedenström. 2010. "Mortality of Bats at Wind Turbines Links to Nocturnal Insect Migration?" *European Journal of Wildlife Research* 56, no. 6: 823–827.

Saugey, D. A., R. L. Vaughn, B. G. Crump, and G. A. Heidt. 1998. "Notes on the Natural History of *Lasiurus Borealis* in Arkansas." *Journal of the Arkansas Academy of Science* 52: 8.

Solick, D., D. Pham, K. Nasman, and K. Bay. 2020. "Bat Activity Rates Do Not Predict Bat Fatality Rates at Wind Energy Facilities." *Acta Chiropterologica* 22: 135.

Somveille, M., A. S. L. Rodrigues, and A. Manica. 2015. "Why Do Birds Migrate? A Macroecological Perspective." *Global Ecology and Biogeography* 24: 664–674.

Stern, S. J. 2009. "Migration and Movement Patterns." In *Encyclopedia of Marine Mammals*, edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen, Second ed., 726–730. Academic Press.

Thompson, M., J. A. Beston, M. Etterson, J. E. Diffendorfer, and S. R. Loss. 2017. "Factors Associated With Bat Mortality at Wind Energy Facilities in the United States." *Biological Conservation* 215: 241–245.

Valdez, E. W., and P. M. Cryan. 2009. “Food Habits of the Hoary Bat (*Lasiurus cinereus*) During Spring Migration Through New Mexico.” *Southwestern Naturalist* 54: 195–200.

Vander Zanden, H. B., D. M. Nelson, M. B. Wunder, T. J. Conkling, and T. E. Katzner. 2018. “Application of Stable Isotopes to Determine Geographic Origin of Terrestrial Wildlife for Conservation Management.” *Biological Conservation* 228: 268–280.

Voigt, C. C., J. Kionka, J. C. Koblitz, P. C. Stilz, G. Pētersons, and O. Lindecke. 2023. “Bidirectional Movements of Nathusius' Pipistrelle Bats (*Pipistrellus nathusii*) During Autumn at a Major Migration Corridor.” *Global Ecology and Conservation* 48: e02695.

Wassenaar, L., and K. Hobson. 2003. “Comparative Equilibration and Online Technique for Determination of Non-Exchangeable Hydrogen of Keratins for Use in Animal Migration Studies.” *Isotopes in Environmental and Health Studies* 39: 211–217.

Weller, T. J., K. T. Castle, F. Liechti, C. D. Hein, M. R. Schirmacher, and P. M. Cryan. 2016. “First Direct Evidence of Long-Distance Seasonal Movements and Hibernation in a Migratory Bat.” *Scientific Reports* 6: 34585.

Wieringa, J. G., J. Nagel, D. M. Nelson, B. C. Carstens, and H. L. Gibbs. 2020. “Using Trace Elements to Identify the Geographic Origin of Migratory Bats.” *PeerJ* 8: e10082.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70202-sup-0001-Supinfo.docx.